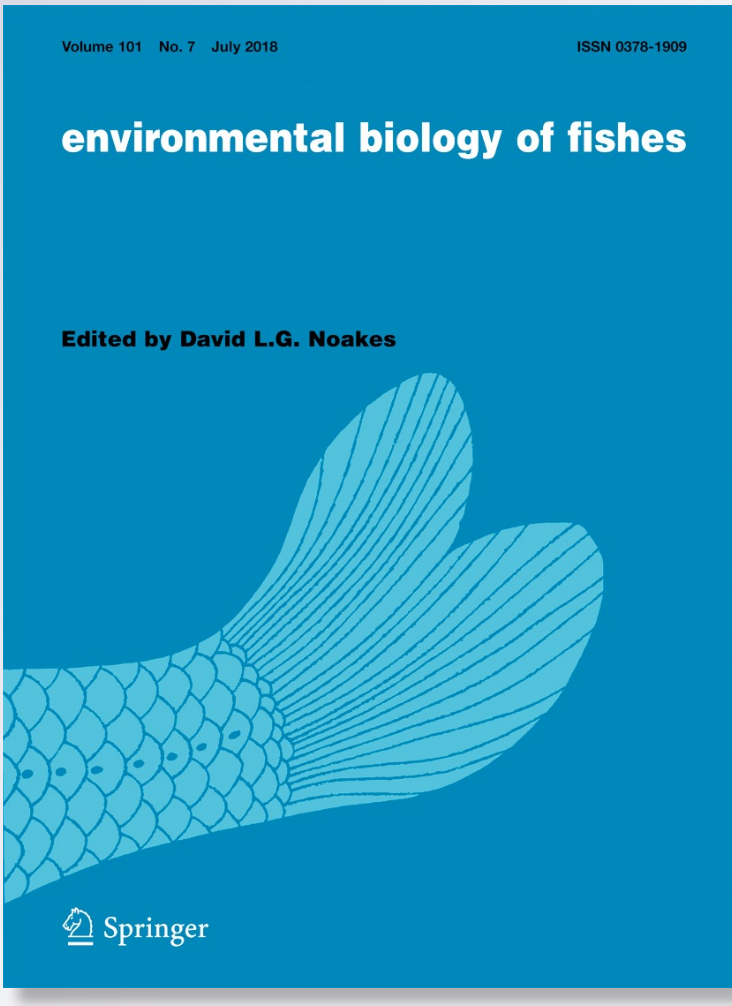
Seasonal feeding ecology of co-existing native and invasive benthic fish along a nearshore to offshore gradient in Lake Michigan

Steven A. Pothoven

Environmental Biology of Fishes

ISSN 0378-1909
Volume 101
Number 7

Environ Biol Fish (2018) 101:1161-1174
DOI 10.1007/s10641-018-0766-7



Springer

Environ Biol Fish (2018) 101:1161–1174
https://doi.org/10.1007/s10641-018-0766-7

Seasonal feeding ecology of co-existing native and invasive benthic fish along a nearshore to offshore gradient in Lake Michigan

Steven A. Pothoven

Received: 4 December 2017 / Accepted: 11 April 2018 / Published online: 17 April 2018

Abstract Relative abundance, diet composition and feeding strategy were determined for three benthic fish, the native deepwater sculpin *Myoxocephalus thompsonii* (Girard, 1851) and slimy sculpin *Cottus cognatus* (Richardson, 1836), and the invasive round goby *Neogobius melanostomus* (Pallas, 1814), along a nearshore to offshore gradient in southeastern Lake Michigan during March–December 2010, 2015, and 2016. Round goby were most abundant in the nearshore (<25 m), slimy sculpin were most abundant in the transitional zone (35–65 m), and deepwater sculpin were most abundant in the offshore zone (>75 m). Despite a large degree of spatial separation, some species did overlap, with slimy and deepwater sculpin occurring in sympatry throughout the year in the offshore and transitional zones, and round goby overlapping with both sculpin species seasonally in the transitional zone. Deepwater sculpin exhibited specialization on *Mysis diluviana* in all depth regions. Slimy sculpin in the offshore reduced diet overlap with deepwater sculpin by specializing on fish eggs during spring and fall, whereas in the transitional depth zone, there was considerable overlap between sculpin species due to the high importance of *Mysis* in diets. The invasive round goby had a mixed diet, with some diet overlap with native sculpin, especially slimy sculpin, in the transitional zone. In the nearshore zone, round goby displayed a generalized diet with many prey contributing to the diet, but the average contribution of any prey was generally low. Spatial separation and variable feeding strategies help reduce, but not eliminate shared resource use amongst these benthic fish in Lake Michigan.

S. A. Pothoven (✉)
Great Lakes Environmental Research Laboratory-National Oceanic and Atmospheric Administration, 1431 Beach St, Muskegon, MI, USA
e-mail: steve.pothoven@noaa.gov

Keywords Sculpin · Round goby · Feeding strategy · Benthic food web · *Mysis*

Introduction

Freshwater sculpins (Cottidae) are an ecologically important group throughout their diverse cool- and coldwater habitats in the northern hemisphere (Adams and Schmetterling 2007). Sculpins can be the dominant species in their ecosystems and are often considered a good indicator species because of their ecological importance and broad trophic interactions (Adams and Schmetterling 2007). Within the Laurentian Great Lakes, efforts are underway to better understand sculpin ecology and interactions with invasive species to facilitate better management of existing sculpin populations and rehabilitation in other lakes (Zimmerman and Krueger 2009). Sculpins are key components of the native deepwater benthic fish community in Lake Michigan, feeding on macroinvertebrates and in turn, providing food for native piscivores, including burbot *Lota lota* (Linnaeus, 1758) and lake trout *Salvelinus namaycush* (Walbaum, 1792) (Fratt et al. 1997; Madenjian et al. 1998). Currently, the two primary species in Great Lakes, including Lake Michigan, are deepwater sculpin *Myoxocephalus thompsonii* (Girard, 1851) and slimy sculpin *Cottus cognatus* (Richardson, 1836) (Scott and Crossman 1998). Deepwater sculpin can account for a large proportion of the offshore fish community in Lake Michigan (Wells 1968; Bunnell et al. 2009). Although slimy sculpin and deepwater sculpin are similar ecologically, their long term coexistence in Lake Michigan appears to have been facilitated through some degree of spatial separation over preferred depth ranges (Madenjian and Bunnell 2008; Hondorp et al. 2011) and differences in food resource partitioning on the basis of prey type and size (Kraft and Kitchell 1986; Hondorp et al. 2011) However, anthropogenic driven changes in the Lake Michigan ecosystem may threaten their co-existence by altering trophic pathways that have provided for their sympatry in the lake.

The offshore Lake Michigan ecosystem has undergone a dramatic transformation over the last two decades. Zebra mussels *Dreissena polymorpha* were found in the lake in the late 1980s, but they were soon replaced by quagga mussels *Dreissena rostriformis bugensis*, which were found in northern Lake Michigan in 1997 (Nalepa et al. 2009). Quagga mussels rapidly spread throughout the lake leading to declines in primary production (Fahnenstiel et al. 2010). Also in the late 1990s, the benthic amphipod *Diporeia* spp. underwent dramatic declines throughout Lake Michigan (Nalepa et al. 2009). *Diporeia* spp. are glacial relicts and had been an important high-energy prey for many fish in Lake Michigan, including deepwater and slimy sculpins (Hondorp et al. 2005). The decline of *Diporeia* spp. led to diet shifts for many fish, including both sculpin species (Hondorp et al. 2005) and was associated with declines in condition for deepwater sculpin (Pothoven et al. 2011). *Diporeia* spp. remain available at much reduced densities only in the deepest regions of Lake Michigan, where they are still consumed by both sculpin species (Mychek-Londer et al. 2013).

By the late 1990s, the invasive benthic fish round goby *Neogobius melanostomus* (Pallas, 1814), native to the Ponto- Caspian region of Eurasia, had spread throughout much of Lake Michigan (Clapp et al. 2001; Kornis et al. 2012). The spread of round goby could have been facilitated by the arrival and proliferation of dreissenid mussels, including quagga mussels, which share a native range with round gobies and can be an important prey (Jude et al. 1995; Vanderploeg et al. 2002). However, dreissenid mussels do not appear to be a pre-requisite for round goby invasion and success (Carman et al. 2006). Competition and behavioral interference by round gobies led to the decline of some native benthivorous fishes, including mottled sculpin *Cottus bairdii* (Girard, 1850) in the nearshore of Lake Michigan (Janssen and Jude 2001). The presence of round goby in the offshore has only been documented fairly recently (Walsh et al. 2007), so there is limited information available on the interactions between deepwater and slimy sculpin with round goby. However, the shared use of the shrimp-like crustacean *Mysis diluviana* (hereafter *Mysis*) is expected to heighten competitive interactions between round goby and native fish in offshore regions of the Great Lakes (Schaeffer et al. 2005; Walsh et al. 2007). *Mysis* have become an increasingly important prey resource for many fish in Lake Michigan following the decline of *Diporeia* spp. (Hondorp et al. 2005).

The goal of this study was to evaluate the nearshore to offshore relative abundance, diet composition, and feeding strategy of deepwater sculpin, slimy sculpin, and round goby in a region of Lake Michigan where all three species are found, and where *Diporeia* spp. have completely disappeared, in order to determine what prey are supporting each species and to provide insight into how these three benthic fish co-exist. Previous work on Lake Michigan indicated that diets of all three species can vary considerably across broad geographic areas of offshore Lake Michigan during the winter (Mychek-Londer et al. 2013), so the goal of this study was to focus on the feeding ecology over the course of the year in a single geographic area across a broad range of depths.

Methods

Sampling took place in southeast Lake Michigan in the vicinity of Muskegon, Michigan, USA as part of various studies to collect forage fish in March–December during 2010, 2015, and 2016. Sampling took place along a nearshore to offshore transect in water depths ranging from 7 to 110 m. Samples were divided into three depth zones, nearshore zone (water depth < 25 m), transitional zone (water depths 35–65 m), and offshore zone (water depths >75 m). The transitional depth zone, as defined, is just below the depth of the thermocline and has historically been an important and productive region within the lake (Nalepa et al. 2000). Fish were collected using a 7.6 m wide skate style bottom trawl with 6.4 mm stretch mesh cod liner towed for 10 min during the day or night. Fish were sorted by species and frozen.

Not all depth zones were sampled for each month and year combination, so we combined all data from a given month across years for analysis because we were primarily interested in seasonal patterns. To assess the spatial distribution of the species across depth zones, we only used night catch rates (#/10 min tow), because some species were rarely caught during daytime trawling. For diet analysis, we used fish collected during the day and night, with most fish coming from night collections (round goby 77%, deepwater sculpin 76%, slimy sculpin 92%). Furthermore, although round goby in a river were found to have diel diet variation (Carman et al. 2006), other evidence from lakes suggests little diel diet variation for either sculpin or round goby (Kraft and Kitchell 1986; Johnson et al. 2008).

In the lab, fish were thawed, measured (TL ± 1 mm), weighed (nearest 0.01 g), and the stomach contents were removed. For round goby, the entire digestive tract was removed because they do not have a distinct stomach. All prey in stomachs were identified and counted. Whole organisms were measured using a microscope-mounted digital camera and image analysis software (Image Pro Premiere V. 9.1). Depending on the prey type, weight-length regressions or a published mean weight were used to estimate the mean dry weight for each prey type (Hawkins and Evans 1979; Nalepa and Quigley 1980; Sell 1982; Makarewicz and Jones 1990; Benke et al. 1999; Conroy et al. 2005; Pothoven unpubl. data). For each fish species, the dry weights of partial prey were assumed to be the same as the mean individual dry weight for a particular prey. Partial prey were counted if intact heads (zooplankton, *Mysis*, Chironomidae) or septum (dreissenid mussels) were present. Weights of all molluscs were determined as shell free dry weight. The mean weight of a given prey type (specific to each predator species) was multiplied by the total number of that respective prey to determine its dry weight contribution to the diet. Diets were expressed as the percent of the total dry weight summed across all fish within each species for a given month and depth zone. For analysis, prey were combined into nine groups, i.e., *Mysis*, Chironomidae, fish eggs, Ostracoda, quagga mussels, other molluscs (Gastropoda and Sphaeridae), Chydoridae, other zooplankton, and other benthic macroinvertebrates (Amphipoda, Oligochaeta). For diet analysis, deepwater sculpin were separated into small ≤80 mm and large >80 mm fish, and round goby into small ≤70 mm and large >70 mm fish, based on two distinct size modes in the length distributions. Slimy sculpin did not have multiple size modes and were not split into size groups.

To evaluate the feeding strategy, an approach proposed by Amundsen et al. (1996) was used, where the prey specific abundance (P_i) is plotted against the frequency of occurrence. Prey specific abundance is the percentage a prey type comprises of all prey items in only those predators in which the prey occurs (Amundsen et al. 1996). We used dry weight diet biomass to determine prey specific abundance. The diagonal from lower left to upper right corner provides a measure of prey importance, with dominant prey in the upper right and rare prey in the lower left. The vertical axis represents the feeding strategy of the predator in terms of specialization and generalization. Predators specialize on prey types on the upper half of the plot, whereas prey types on the lower half of the plot represent a generalized feeding strategy. Prey points in the upper left indicate specialization by individuals whereas points in the upper right indicate a dominant prey of the overall population (Amundsen et al. 1996).

Analysis of similarities (ANOSIM) was used to test for differences in standardized diet composition among species in each depth zone for each month where they co-occurred. This approach is analogous to an ANOVA, with a non-parametric permutation applied to a rank similarity matrix of samples (Clarke and Warwick 2001). Diet composition, standardized as percent of total dry weight, was square root transformed to down-weight highly abundant species (Clarke and Warwick 2001) and used to create a Bray-Curtis similarity matrix for ANOSIM. R-values from ANOSIM range from −1 to +1, and generally lie between 0, where groups are indistinguishable and + 1, where all similarities within groups are less than any similarity between groups (Clarke and Gorley 2001). Negative R-values indicate greater dissimilarity among replicates within a sample than between samples (Chapman and Underwood 1999). R-values values provide an absolute measure of how separated groups are, with R-values <0.25 indicating almost no separation between groups, R-values of 0.25–0.5 indicating different groups but with considerable overlap, R-values of 0.5 to 0.75 indicating clearly different group with some overlap, and R-values >0.75 indicating clear separation between groups (Clarke and Gorley 2001, 2006). We used R-values rather than *p*-values from ANOSIM tests because this is the most useful measure and provides an absolute measure of how separated the groups are (Clarke and Gorley 2001, 2006). ANOSIM was performed using Primer v5.2.9.

Results

Relative abundance

In the nearshore depth zone, almost nothing was caught except round gobies, which accounted for 94–100% of fish collected in nearshore trawls each month (Fig. 1). In the transitional depth zone, all three species were represented, with slimy sculpin generally accounting for majority of catch (Fig. 1). Deepwater sculpin were generally a minor component of the catch in the transitional zone, accounting for 7–16% of the catch except in September and December, when none were collected at night. Round goby were mainly caught in the transitional zone in the fall and spring, accounting for 8–14% of the catch in the spring and 23–57% of the catch in the fall. The offshore depth zone was dominated by deepwater sculpin, which accounted for 92–97% of the catch, with slimy sculpin accounting for the remainder of the catch and round goby almost entirely absent from region (Fig. 1).

Diet composition

In the nearshore, small round goby (≤ 70 mm) had diverse diets, with chydorids, ostracods, quagga mussels, fish eggs, chironmids, zooplankton, and other molluscs all accounting for at least 10% of the diet in at least one month (Fig. 2). Ostracods were consistently important each month along with quagga mussels/other molluscs. For large round goby in the nearshore, important prey groups were similar to those of small round goby, with quagga mussels/molluscs consistently important each month, but not ostracods. Quagga mussels/other molluscs combined

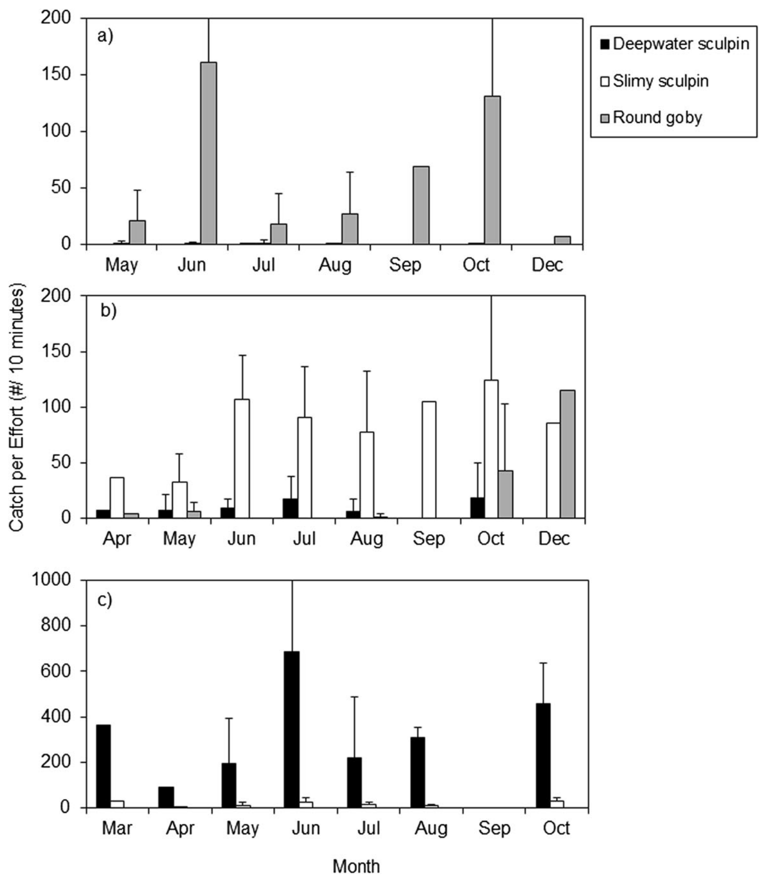


Fig. 1 Mean nighttime catch per effort (#/10 min bottom trawl) ± 1 SD by month for deepwater sculpin, slimy sculpin, and round goby in (**a**) nearshore (< 25 m), (**b**) transitional (35–65 m), and (**c**) offshore (> 75 m) depth zones in southeast Lake Michigan

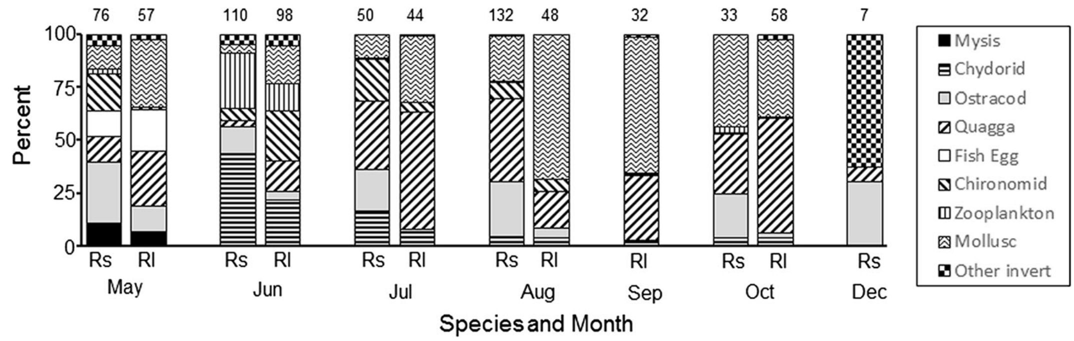


Fig. 2 Diet composition (% dry weight) by month for small round goby (Rs) and large round goby (Rl) in the nearshore depth zone (< 25 m) of southeast Lake Michigan. The number of fish with food in their stomachs is given above each bar

were generally more important in July-Oct than May–June for both sizes of round gobies and were more important for large than small round gobies each month.

In the transitional depth zone, the most abundant fish, slimy sculpin, ate mostly *Mysis* (85–98%), with chironmids the most common secondary prey (Fig. 3). Mostly small deepwater sculpin were found in this depth region, and their diets were almost exclusively *Mysis* (97–100%) (Fig. 3). Both small and large round goby were caught in the transitional zone, mostly in the spring and fall, and diets were varied, especially in the fall (Fig. 3). Small round goby ate mostly ostracods in the spring and ostracods, other molluscs, *Mysis*, and quagga mussels in the fall. Large round goby ate mostly *Mysis* in the spring, ostracods, quagga mussels, zooplankton (mostly *Bythotrephes longimanus*), and other invertebrates (mostly amphipods) in the summer, and ostracods, quagga mussels, other molluscs, *Mysis*, and fish eggs in the fall.

In the offshore zone, *Mysis* composed 98–100% of the small deepwater sculpin diets and 82–100% of large deepwater sculpin diets, with fish eggs being the only other prey that accounted for >10% of the diet (Fig. 4). Slimy sculpin diets were mainly fish eggs or *Mysis*, with fish eggs primarily important in the spring and fall (Fig. 4).

Feeding strategy

Large round goby in the nearshore depth zone generally had a generalist diet, with the most important prey eaten by majority of fish, but the average contribution of these prey to the diet being relatively low (Fig. 5). In the spring, a few individual large round goby did specialize on a particular prey, and in late summer, other molluscs were specialized upon by a relatively large fraction of the large round goby population. Small round goby in the nearshore zone also demonstrated a generalized diet,

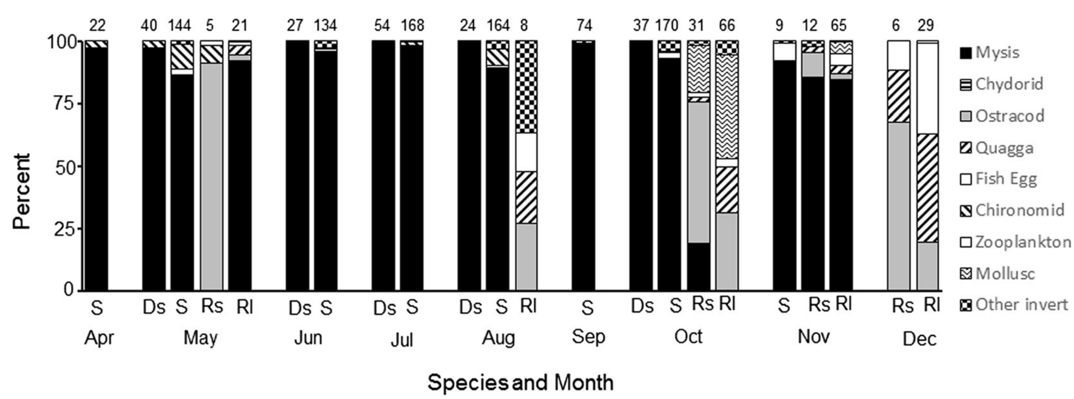


Fig. 3 Diet composition (% dry weight) by month for slimy sculpin (S), small deepwater sculpin (Ds), small round goby (Rs) and large round goby (Rl) in the transitional depth zone (35–65 m) of southeast Lake Michigan. The number of fish with food in their stomachs is given above each bar

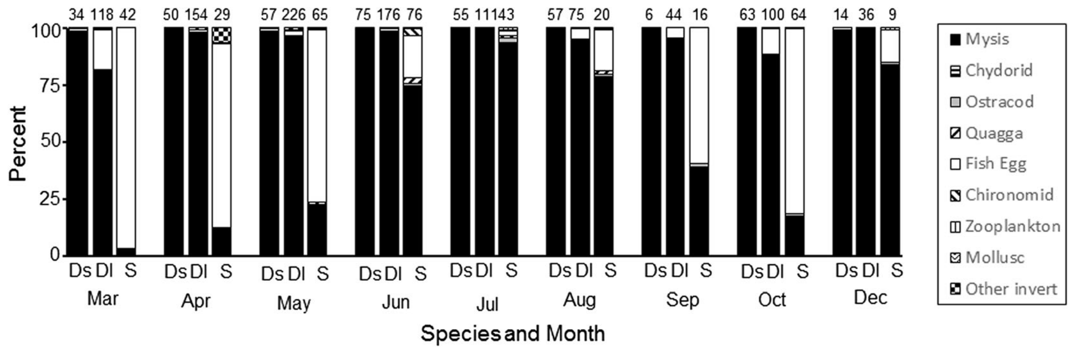


Fig. 4 Diet composition (% dry weight) by month for large deepwater sculpin (Dl), small deepwater sculpin (Ds), and slimy sculpin (S) in the offshore depth zone (>75 m) of southeast Lake Michigan. The number of fish with food in their stomachs is given above each bar

with only a few instances of individual specialization on prey in the spring (Fig. 5).

Slimy sculpin in the transitional depth zone generally had a mixed feeding strategy (Fig. 6). *Mysis* were a fairly important species at the population level each month, with 49–78% of slimy sculpin consuming *Mysis*. Some prey like chironomids and zooplankton were eaten by a high percentage of fish, but accounted for little of those fish's diets, whereas prey like fish eggs, quagga mussels, other molluscs, and other invertebrates were only eaten by a few individuals but accounted for most of those fish's diets. Small deepwater sculpin in the transitional depth zone had a feeding strategy that specialized on *Mysis* at the population level with very limited individual specialization or generalized feeding on other prey (Fig. 6). Large round goby in the transitional depth zone had a mixed feeding strategy that varied among months. If *Mysis* were eaten, they were a specialized prey of a small portion of the large round goby population. The role of quagga mussels was variable among months, i.e., they were dominant at population level in December, but a generalized prey or a specialized prey of a few individuals for other months. Ostracods were a generalized prey that was consistently eaten by a high proportion of large round goby in this zone, but only accounted for small part of overall diet. The feeding strategy of small round goby in the transitional depth zone was variable, with ostracods the dominant prey at population level for May, October, and December, but a more generalized prey in November (Fig. 6). At certain times, small round goby demonstrated generalized feeding on chironomids (May) or quagga mussels (December) and some individual specialization *Mysis* (October/November) or other molluscs (October).

In the offshore depth zone, both small and large deepwater sculpin demonstrated population specialization on *Mysis*, which was eaten by most fish and accounted for most of the diet. There were only a few instances of individual specialization on other invertebrates, chironomids or fish eggs (Fig. 7). Slimy sculpin in the offshore zone had more variable feeding strategy than deepwater sculpin, shifting from population specialization on fish eggs in March–May to a more mixed feeding strategy with fish eggs becoming a prey specialized on by individuals rather than the population and *Mysis* increasing in importance (Fig. 7). *Mysis* however, were largely a prey specialized on by individuals even after its increase in importance, as generally <50% of slimy sculpin ate this prey. Other prey of slimy sculpin were eaten generally, i.e., by many individuals but accounting for little of the diet (ostracods and zooplankton) or specialized on by a few individuals (quagga mussels), or both strategies, depending on the month (chironomids).

Diet overlap

In the nearshore depth zone, diet assemblages of small and large round gobies generally overlapped ($R < 0.21$), with only slight separation between these groups being found in October ($R = 0.29$; Table 1). In the transitional depth zone, prey assemblages consumed by the most frequently co-occurring species in our sampling, small deepwater sculpin and slimy sculpin, were indistinguishable ($R < 0$; Table 1). In fact, there was more variation within a species diet than between species as evidenced by the negative R-

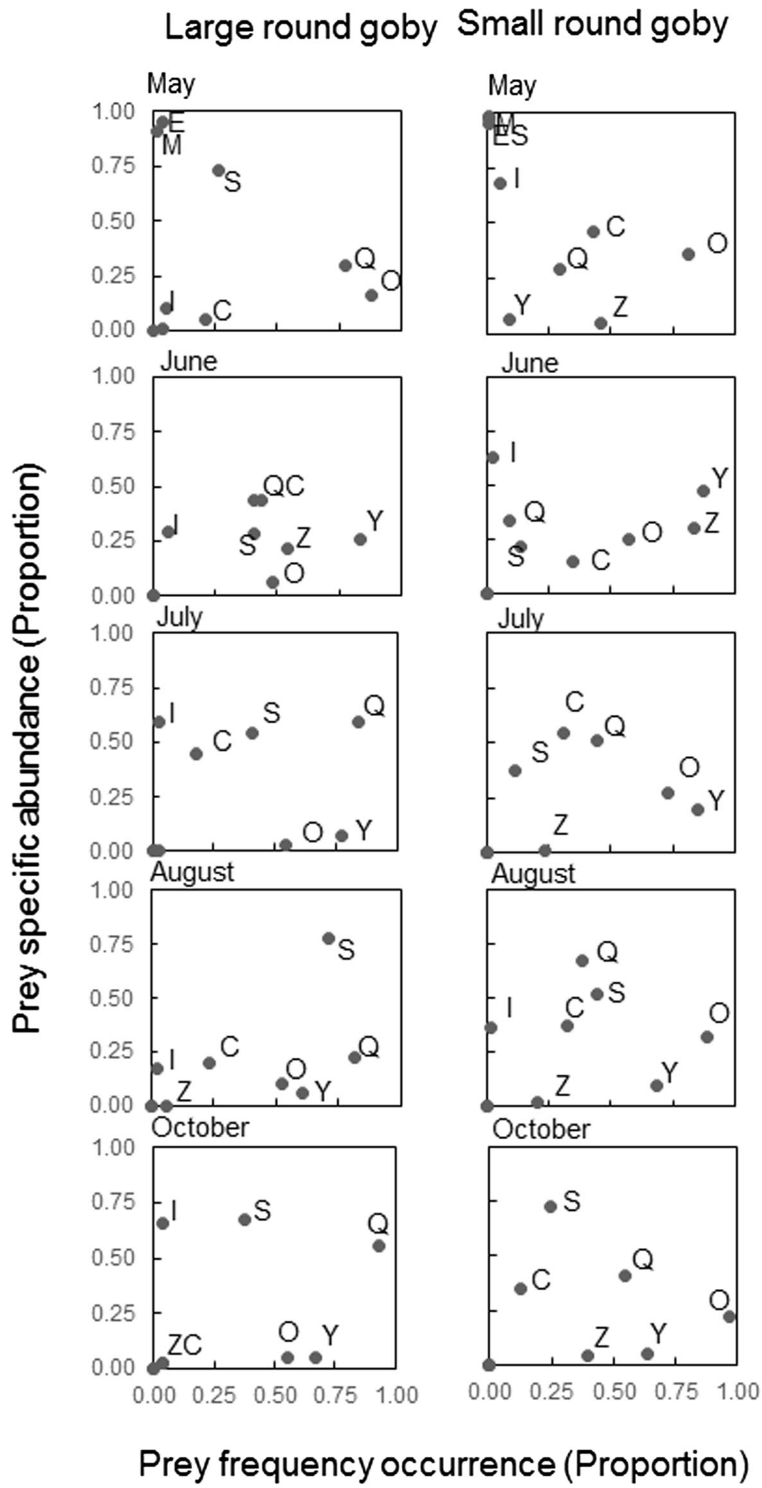


Fig. 5 Feeding strategy plot (prey specific abundance on a percent dry weight basis plotted against frequency of occurrence, Amundsen et al. 1996) for small and large round goby in the nearshore depth zone of southeastern Lake Michigan. The diagonal from lower left to upper right corner provides a measure of prey importance, with dominant prey in the upper right and unimportant prey in the lower left. The vertical axis represents the feeding strategy of the fish in terms of specialization (upper part of plot) and generalization (lower part of plot). Prey points in the upper left indicate specialization by individuals whereas points in the upper right indicate a dominant prey of the overall population (Amundsen et al. 1996). M = Mysis, E = fish egg, C = chironomid, Q = quagga mussel, O = ostracod, Y = chydorid, Z = other zooplankton, S = other molluscs, I = other benthic invertebrates

values. By contrast, diet assemblages between small deepwater sculpin and small and large round goby were well separated ($R > 0.82$), except in May, when there was considerable overlap between the two groups ($R = 0.44$). Diet assemblages of slimy sculpin and small and large round gobies generally had

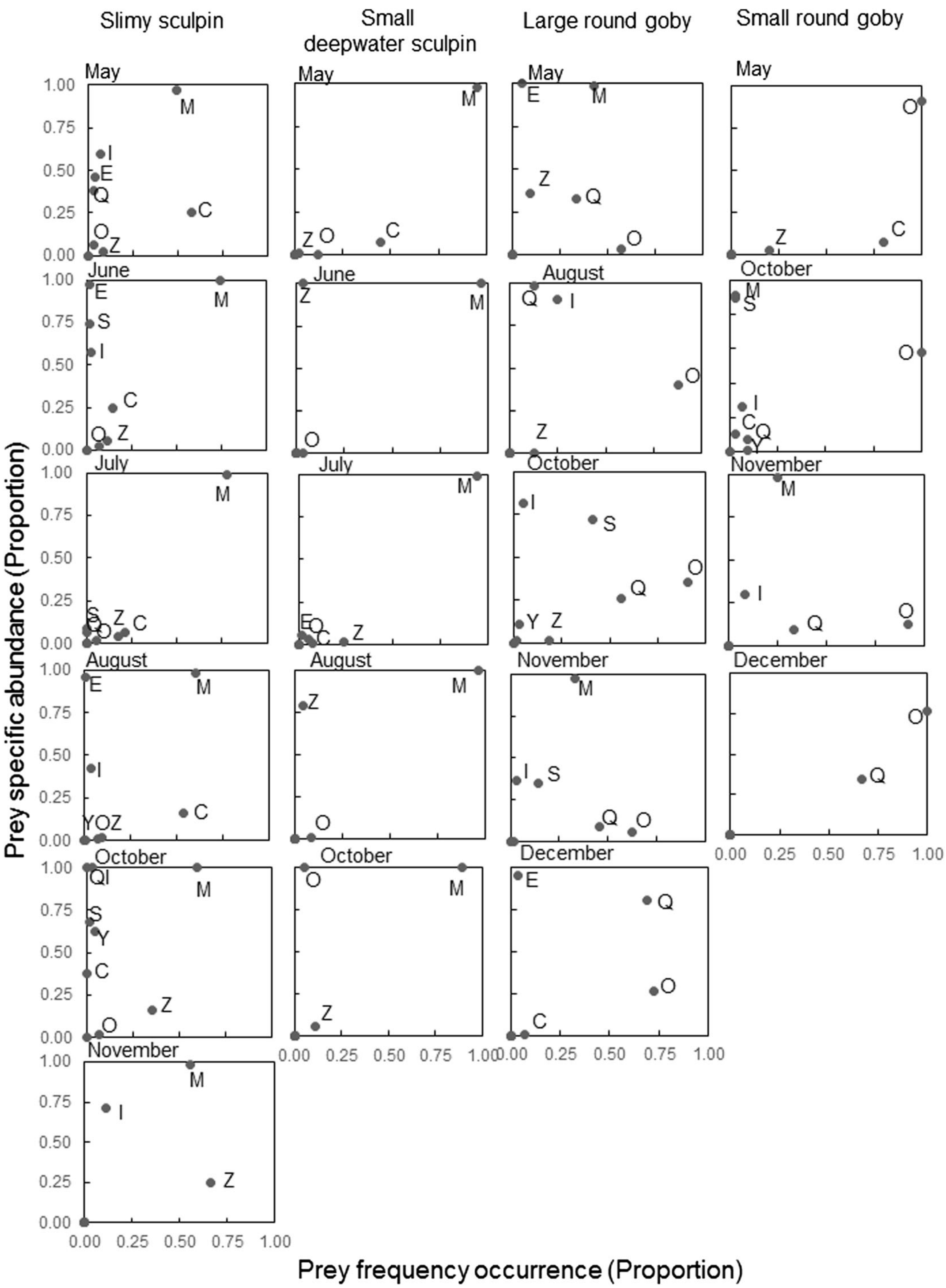


Fig. 6 Feeding strategy plot (prey specific abundance on a percent dry weight basis plotted against frequency of occurrence, Amundsen et al. 1996) for slimy sculpin, small deepwater sculpin, small and large round goby in the transitional depth zone of southeastern Lake Michigan. M = Mysis, E = fish egg, C = chironomid, Q = quagga mussel, O = ostracod, Y = chydorid, Z = other zooplankton, S = other molluscs, I = other benthic invertebrates

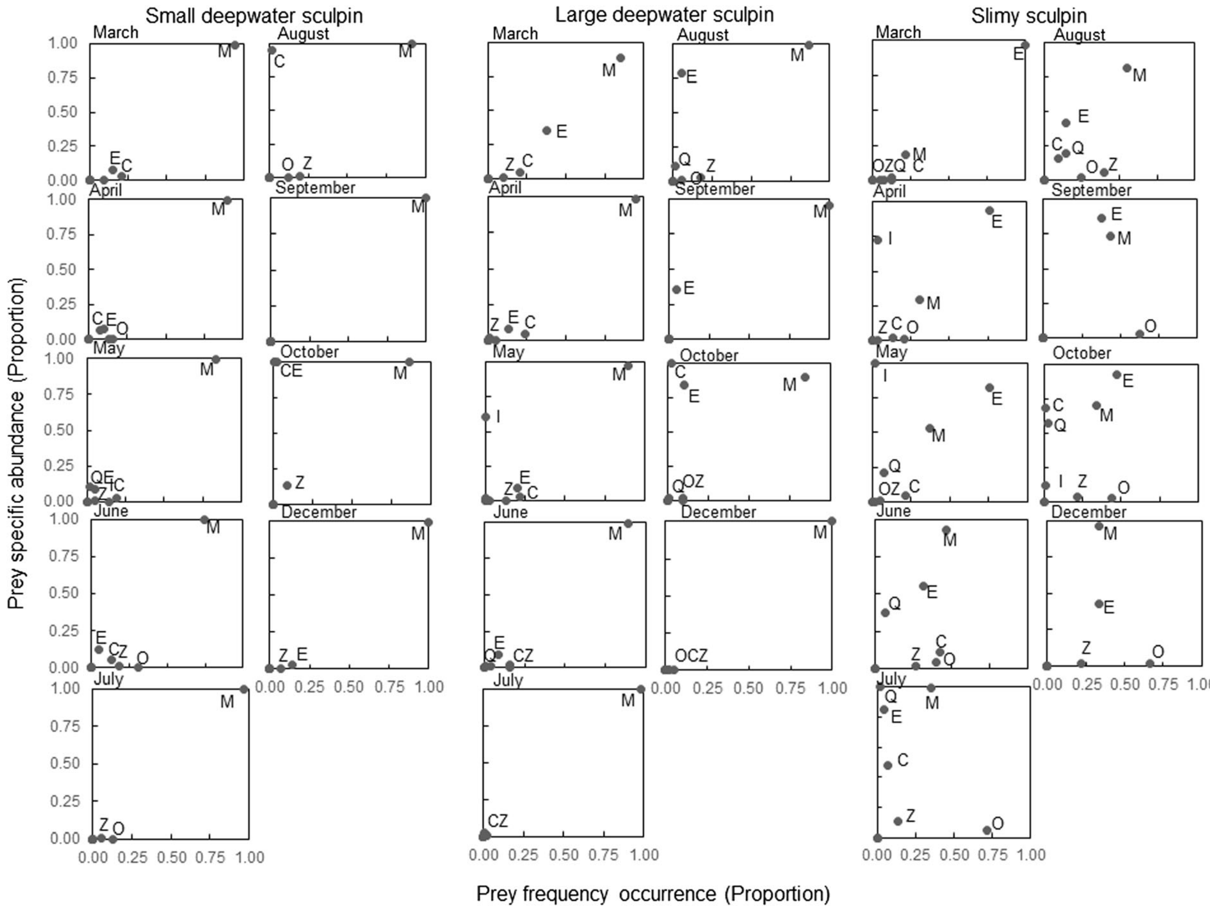


Fig. 7 Feeding strategy plot (prey specific abundance on a percent dry weight basis plotted against frequency of occurrence, Amundsen et al. 1996) for small and large deepwater sculpin and slimy sculpin in the offshore depth zone of southeastern Lake Michigan. M = Mysis, E = fish egg, C = chironomid, Q = quagga mussel, O = ostracod, Y = chydorid, Z = other zooplankton, S = other molluscs, I = other benthic invertebrates

considerable overlap ($R < 0.49$), although there were months where slimy sculpin was more clearly differentiated from both large ($R = 0.57$, August) and small ($R = 0.59$, November) round gobies. Small and large goby diets were indistinguishable in the transitional depth zone ($R < 0.05$).

In the offshore depth zone, small and large deepwater sculpin diet assemblages were indistinguishable ($R < 0.12$; Table 1). Overlap in diet assemblages of large deepwater sculpin with slimy sculpin in the offshore zone varied among months, ranging from no overlap in December ($R = 0.84$) to considerable overlap in June, August and October ($R < 0.36$). For small deepwater sculpin and slimy sculpin, diet overlap varied among months, ranging from no overlap in March ($R = 0.94$) to indistinguishable diets in June and September ($R < 0.14$).

Discussion

We observed that there was a large degree of spatial separation among round goby, slimy sculpin, and deepwater sculpin along the depth gradient from the shallow nearshore to the deep offshore of southeast Lake Michigan. That is, CPE for each species tended to be concentrated in a single depth zone, where that particular species was the dominant component of the catch. Historically, competition between deepwater and slimy sculpin has likely been mitigated through some degree of depth segregation, with slimy sculpin more prevalent at shallower depths and deepwater sculpin more abundant further offshore (Kraft and Kitchell 1986; Madenjian and Bunnell 2008; Hondorp et al. 2011). Differing predation pressures (Madenjian et al. 2005) and prey preferences that help reduce competition

Table 1 Diet overlap between pairs of species groups based on R-values from ANOSIM by month for each of the three depth zones in southeastern Lake Michigan

Depth zone	Species	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Nearshore	S. goby - L. goby	–	–	0.21	0.15	0.22	0.16	–	0.29	–	–
Transitional	Slimy - L. goby	–	–	0.30	–	–	0.57	–	0.49	0.39	–
	Slimy – S. goby	–	–	0.24	–	–	–	–	0.44	0.59	–
	Slimy – S. deep	–	–	−0.06	−0.15	−0.08	−0.07	−0.10	–	–	–
	S. deep – L. goby	–	–	0.44	–	–	0.90	–	0.84	–	–
	S. deep – S. goby	–	–	0.91	–	–	–	–	0.82	–	–
	L. goby – S. goby	–	–	0.08	–	–	–	–	0.05	−0.08	−0.07
Offshore	S. deep – L. deep	−0.12	0.00	−0.02	0.12	0.07	−0.01	−0.04	−0.03	–	0.10
	S. deep – Slimy	0.94	0.56	0.39	0.09	0.51	0.33	0.14	0.30	–	0.61
	L. deep - Slimy	0.56	0.70	0.53	0.36	0.71	0.29	0.74	0.32	–	0.84

R-values <0.25 indicate almost no separation between groups, R-values of 0.25–0.5 indicate different groups but with considerable overlap, R-values of 0.5 to 0.75 indicate clearly different group with some overlap, and R-values >0.75 indicate clear separation between groups (Clarke and Gorley 2001, 2006). Negative R-values indicate more dissimilarity within a group than between groups

S. goby, small round goby; *L goby*, large round goby; *Slimy*, slimy sculpin; *S. deep*, small deepwater sculpin; *L. deep*, large deepwater sculpin

(Wells 1968; Kraft and Kitchell 1986; Hondorp et al. 2011) are possible mechanisms behind the depth distributions of the two sculpin species.

Invasive round gobies were prevalent in the nearshore zone and thus were largely spatially segregated from the two sculpin species, but there was evidence that round goby moved deeper into the transitional depth in the fall and were still present in the spring, suggesting that they overwinter in deeper areas where they experience more overlap with sculpin. In their native range, round gobies migrate offshore in winter, and there is some evidence for seasonal movement of round goby into the offshore (55–130 m) from other studies in the Great Lakes (Schaeffer et al. 2005; Walsh et al. 2007). There is also evidence that in some areas of Lake Michigan, round goby co-occur with both sculpin species in the offshore (73–128 m) throughout the winter (Mychek-Londer et al. 2013).

Despite a large degree of spatial separation, some fish did overlap, with slimy and deepwater sculpin occurring in sympatry throughout the year in the offshore and transitional depth zones, and round goby overlapping with both sculpin species seasonally in the transitional depth zone. Round goby are known to have broad diets and plasticity enabling them to take advantage of various production pathways, which likely has helped facilitate their successful establishment in the lake (Pettitt-Wade et al. 2015; Foley et al. 2017; Kornis et al. 2017). As the invasive round goby was documented further offshore in the Great Lakes, there has been concern that it would compete with native sculpins for food, particularly *Mysis* which became a critical food source after *Diporeia* spp. declined (Schaeffer et al. 2005; Walsh et al. 2007). However, Mychek-Londer et al. (2013) found little diet overlap (based on Shoener's index) between sculpins and round goby in the offshore (73–128 m) of Lake Michigan in the winter. We found that round goby had a mixed feeding strategy when found in the transitional depth zone, and *Mysis* were a prey specialized on by individuals, not a large fraction of the population. This mixed feeding strategy appeared to greatly reduce diet overlap with deepwater sculpin in the transitional depth zone. However, there was still some diet overlap between round goby and slimy sculpin in the transitional depth zone, due to overlap with *Mysis* and other prey that were specialized on by individuals of both species, especially in the spring. Round goby are also an aggressive fish that could compete with slimy sculpin for spawning habitat and whose behavior has been implicated in the decline of other native fish species (Janssen and Jude 2001; Bergstrom and Mensinger 2009), so their impacts on native fish likely extends beyond simple shared resource use.

Diet overlap for the most consistently co-occurring species in the offshore and transitional depth zones, deepwater and slimy sculpin, depended on season and/or depth zone. In the transitional depth zone, there was complete overlap between slimy sculpin and deepwater sculpin diets, with *Mysis* a key component of the diet for both species. In the offshore, where slimy sculpin were a minor component of the sculpin community, their feeding strategy varied seasonally and was different than in the transitional depth, i.e., fish eggs were a dominant prey in the spring with more individual specialization or generalized feeding in the summer and fall with *Mysis* increasing in importance. This variable feeding strategy of slimy sculpin across seasons in the offshore resulted in variable diet overlap with deepwater sculpin, ranging from completely different diets to high overlap. Similarly, Mychek-Londer et al. (2013) found overlap between deepwater sculpin and slimy sculpin diets in winter at two of three offshore sites in Lake Michigan.

Prior to the complete disappearance of *Diporeia* spp. in the region, Hondorp et al. (2011) found that slimy sculpin and deepwater sculpin mitigated competitive interactions through differing prey and prey size selectivity. For example, deepwater sculpin selected *Mysis* over *Diporeia* spp. and selected larger *Diporeia* spp. than slimy sculpin, which preferred *Diporeia* spp. to *Mysis* (Hondorp et al. 2011). As *Diporeia* spp. declined, there was concern that slimy sculpin would be particularly vulnerable given their reliance on this prey. In fact, declines of slimy sculpin in Lake Ontario were linked to the disappearance of *Diporeia* spp. (Owens and Dittman 2003). However, in Lake Michigan, slimy sculpin diets indicate that they can persist even as diet composition shifts to *Mysis* and they can adjust feeding strategy based on their interaction with deepwater sculpin. Slimy sculpin have a broad geographic range across North America and are able to exploit a broad range of prey across environments, unlike deepwater sculpin which are glacial relicts and always found in sympatry with glacial relict prey, most often *Mysis* and *Diporeia* spp. (Sheldon et al. 2008). Indeed, deepwater sculpin diets in this study were almost entirely focused on *Mysis* and feeding strategy did not vary between depth zones, regardless of whether deepwater sculpin were the dominant fish or not.

Following decline of *Diporeia* spp., the importance of *Mysis* in diets increased for sculpin as well as other fish including bloater *Coregonus hoyi* (Milner, 1874) and alewife *Alosa psuedoharengus* (Wilson, 1811) (Hondorp et al. 2005; Pothoven and Madenjian 2008; Pothoven and Bunnell 2016). Modelling efforts indicate that *Mysis* is currently a critical keystone species within Lake Michigan, and deepwater sculpin are the primary predator of this important prey species (Rogers et al. 2014). *Mysis* in southeast Lake Michigan underwent declines of 82% and 54% at a 45 m and 110 m site, respectively, between 1995 and 2002 and 2007–2015 (Pothoven and Vanderploeg 2017). These declines occurred despite declining planktivorous fish abundance, including sculpins, suggesting a decoupling of *Mysis* abundance with predator abundance due to declining productivity and the loss of the alternative prey *Diporeia* spp. (Pothoven and Bunnell 2016; Pothoven and Vanderploeg 2017).

The transitional depth zone, where all three fish species were found in sympatry, has historically been an important and productive region within the lake. This region, as defined, is just below the depth of the thermocline where there are relatively stable thermal conditions and food inputs to the benthic region are maximized (Nalepa et al. 2000). This region had supported maximum benthic invertebrate biomass in Lake Michigan, including *Diporeia* spp., whose densities exceeded 10,000/m^2 in 1980s but declined to near zero by 2005 (Nalepa et al. 1998, 2009). After declines of *Diporeia* spp., this region also supported the maximum biomass of dreissenid mussels in the lake (Nalepa et al. 2010).

In addition to being a productive region, the transitional depth zone is an important region for early life history of deepwater sculpin. Deepwater sculpin larvae hatch offshore in November to August, peaking in March (Geffen and Nash 1992). These larvae are pelagic until they reach 20–40 mm, generally around September, when they settle in water as deep as shallowest fringe of the adult population (around 50 m), moving further offshore as they grow (Geffen and Nash 1992). Newly settled deepwater sculpin formerly fed on the abundant *Diporeia* spp. and *Mysis* in this region, but now only *Mysis* are available. Indeed, 88% of deepwater sculpin <40 mm in this region in our study ($n = 18$) had eaten *Mysis*, which accounted for 99% of the diet biomass, and no other prey was found in more than 28% of the fish stomachs. Bottlenecks in a fish's life history occur when there are changes in habitat or diet, often during early life, and can regulate populations (Elliott 1994). The period when deepwater sculpin larvae settle to the lake bottom could certainly be considered a bottleneck for recruitment, especially after *Diporeia* spp. disappeared and *Mysis*, which also support the abundant slimy sculpin population, also declined in abundance (Pothoven and Vanderploeg 2017). Furthermore, *Mysis* biomass in the transitional zone is quite low and is only a fifth of that found in the offshore region (Pothoven and Vanderploeg 2017).

The seasonal population specialization on fish eggs by slimy sculpin in the offshore region could have food web implications for fish recruitment in the region. Most eggs eaten were likely incubating eggs from deepwater sculpin and bloater (Mychek-Londer et al. 2013). However, despite some evidence that slimy sculpin predation on eggs could limit bloater recruitment in Lake Michigan, other undetermined factors appeared important as well (Bunnell et al. 2014). Slimy sculpin consumption of eggs from either deepwater sculpin or bloater could have a disproportionately high impact on recruitment of those species due to their low population relative to historic patterns (Mychek-Londer et al. 2013).

The prevalence of round gobies and their generalized diets highlight how trophic pathways in Lake Michigan have been altered by invasive species and declines in native prey such as *Diporeia* spp. Slimy sculpin were previously more common in the nearshore zone, where their diets consisted of a high percentage of *Diporeia* spp., along with fish eggs and chironomids (Kraft and Kitchell 1986; Pothoven, unpublished data). In turn, slimy sculpin were eaten by lake trout and adult yellow perch (Pothoven, unpublished data). Lake trout and yellow perch *Perca flavescens* (Mitchill, 1814) still consume the primary benthic fish in the nearshore, round goby (Truemper et al. 2006; Happel et al. 2017), but round goby in the nearshore rely heavily on a wide variety of benthic prey, especially ostracods and quagga mussels/other molluscs (Kornis et al. 2012). Thus, the pathways supporting piscivore production in the nearshore have drastically changed. Interestingly, quagga mussels appear to be more important to round goby diets in the nearshore than the transitional zone, even though quagga mussel biomass is much higher in the transitional zone (Nalepa et al. 2010). Also the high occurrence of ostracods in round goby diets is somewhat surprising given their rarity in other forage fish diets, although this was also noted in Lake Huron (Schaeffer et al. 2005). The ability to use a wide variety of prey resources and flexible feeding strategies are likely important for the success of round gobies as an invasive species.

This study indicates that deepwater sculpin, slimy sculpin, and round goby co-existence in a region of southeastern Lake Michigan is largely facilitated by spatial separation along the depth gradient from nearshore to offshore, as well as different feeding strategies and prey. Both round goby and slimy sculpin appeared fairly flexible in diets and feeding strategy which helped reduce, but not eliminate, diet overlap when found in sympatry. However, deepwater sculpin appear fairly inflexible in feeding strategy and diets, relying almost entirely on one prey, *Mysis*. Thus, it will be important to continue to evaluate diets and feeding strategies of sculpin and gobies as the role of round goby in the food web continues to develop. Food web changes in Lake Michigan in the 1960s resulted in the near disappearance of another offshore sculpin species, the spoonhead sculpin *Cottus ricei* (Nelson, 1876), highlighting the potential vulnerability of these profundal fish species following ecological changes. On the other hand, after being considered extinct, deepwater sculpin have made a resurgence in Lake Ontario despite the disappearance of *Diporeia* spp. and proliferation of round goby into the offshore (Weidel et al. 2017), indicating that the direction of food web changes can be unexpected as well.

Acknowledgements We would like to thank those that provided help in the field and laboratory, including the crew of the RV Laurentian, D. Ruberg, J. Rediske, A. Zantello, J. Elliott, and A. Dunnuck. Handling of fishes followed the guidelines provided in the "Guidelines for the use of fishes in research" published by the American Fisheries Society, Bethesda, MD. This is GLERL contribution # 1881.

References

Adams SB, Schmetterling DA (2007) Freshwater sculpins: Phylogenetics to ecology. T Am Fish Soc 136:1736–1741

Amundsen PA, Gabler HM, Staldvik FJ (1996) A new approach to graphical analysis of feeding strategy from stomach contents data–modification of the Costello (1990) method. J Fish Biol 48:607–614

Benke AC, Huryn AD, Smock LA, Wallace JB (1999) Length-mass relationships for freshwater macroinvertebrates in North America with particular reference to the southeastern United States. J N Am Benthol Soc 18:308–343

Bergstrom MA, Mensinger AF (2009) Interspecific resource competition between the invasive round goby and three native species: logperch, slimy sculpin, and spoonhead sculpin. T Am Fish Soc 138:1009–1017

Bunnell DB, Madenjian CP, Holuszko JD, Adams JV French JRP III (2009) Expansion of *Dreissena* into offshore waters of Lake Michigan and potential impacts on fish populations. J Great Lakes Res 35:74–80

Bunnell DB, Mychek-Londer JG, Madenjian CP (2014) Population-level effects of egg predation on a native planktivore in a large freshwater lake. Ecol Freshw Fish 23:604–614

Carman SM, Janssen J, Jude DJ, Berg MB (2006) Diel interactions between prey behavior and feeding in an invasive fish, the round goby, in a north American river. Freshw Biol 51:742–755

Chapman MG, Underwood AJ (1999) Ecological patterns in multivariate assemblages information and interpretation of negative values in ANOSIM tests. Mar Ecol Prog Ser 180:257–265

Conroy JD, Edwards WJ, Pontius RA, Kane DD, Zhang H, Shea JF, Richey JN, Culver DA (2005) Soluble nitrogen and phosphorus excretion of exotic freshwater mussels (*Dreissena* spp.): potential impacts for nutrient remineralisation in western Lake Erie. Freshw Biol 50:1146–1162

Clapp DF, Schneeberger PJ, Jude DJ, Madison G, Pistis C (2001) Monitoring round goby (*Neogobius melanostomus*) population expansion in eastern and northern Lake Michigan. J Great Lakes Res 27:335–341

Clarke KR, Gorley RN (2001) Primer v5: User Manual/Tutorial. Primer-E-LTD, Plymouth, UK

Clarke KR, Gorley RN (2006) Primer v6: user manual/tutorial. Primer-E-LTD, Plymouth, UK

Clarke KR, Warwick RM (2001) Changes in marine communities: an approach to statistical analysis and interpretation, primer-E, 2nd edn. Primer-E-LTD, Plymouth, UK

Elliott JM (1994) Quantitative ecology and the brown trout. Oxford University Press, Oxford

Fahnenstiel GL, Pothoven SA, Nalepa TF, Vanderploeg HA, Klarer D, McCormick M, Scavia D (2010) Recent changes in primary production and phytoplankton in the offshore region of southeastern Lake Michigan. J Great Lakes Res 36(S3):20–29

Foley CJ, Henebry ML, Happel A, Bootsma HA, Czesny SJ, Janssen J, Jude DJ, Rinchard J, Höök TO (2017) Patterns of integration of invasive round goby (*Neogobius melanostomus*) into a nearshore freshwater food web. Food Webs 10:26–38

Fratt TW, Coble DW, Copes F, Bruesewitz RE (1997) Diet of burbot in Green Bay and western Lake Michigan with comparison to other waters. J Great Lakes Res 23:1–10

Geffen AJ, Nash RDM (1992) The life-history strategy of deepwater sculpin, *Myoxocephalus thompsoni* (Girard), in Lake Michigan: dispersal and settlement patterns during the first year of life. J Fish Biol 41(Suppl B):101–110

Happel A, Jonas JL, McKenna PR, Rinchard J, He JZ, Czesny SJ (2017) Spatial variability of lake trout diets in lakes Huron and Michigan revealed by stomach content and fatty acid profiles. Can J Fish Aquat Sci 75:95–105. https://doi.org/10.1139/cjfas-2016-0202

Hawkins BE, Evans MS (1979) Seasonal cycles of zooplankton biomass in southeastern Lake Michigan. J Great Lakes Res 5:256–263

Hondorp DW, Pothoven SA, Brandt SB (2005) Influence of *Diporeia* density on diet composition, relative abundance, and energy density of planktivorous fishes in Southeast Lake Michigan. T Am Fish Soc 134:588–601

Hondorp DW, Pothoven SA, Brandt SB (2011) Feeding selectivity of slimy sculpin *Cottus cognatus* and Deepwater sculpin *Myoxocephalus thompsonii* in Southeast Lake Michigan: implications for species coexistence. J Great Lakes Res 37:165–172

Janssen JJ, Jude DJ (2001) Recruitment failure of mottled sculpin *Cottus bairdi* in the Calumet Harbor, southern Lake Michigan, induced by the newly introduced round goby *Neogobius melanostomus*. J Great Lakes Res 27:31–328

Johnson JH, McKenna JE, Nack CC, Chalupnicki MA (2008) Diel diet composition and feeding activity of round goby in the nearshore region of Lake Ontario. J Freshw Ecol 23:607–612

Jude DJ, Janssen J, Crawford G (1995) Ecology, distribution, and impact of the newly introduced round and tubenose gobies on the biota of the St. Clair and Detroit rivers. In: Munawar M, Edsall T, Leach J (eds) The Lake Huron ecosystem: ecology, fisheries and management. SPB academic publishing, Amsterdam, pp 447–460

Kornis MS, Mercado-Silva N, Vander Zanden MJ (2012) Twenty years of invasion: a review of round goby *Neogobius melanostomus* biology, spread and ecological implications. J Fish Biol 80:235–285

Kornis MS, Weidel BC, Vander Zanden MJ (2017) Divergent life histories of invasive round gobies (*Neogobius melanostomus*) in Lake Michigan and its tributaries. Ecol Freshw Fish 26:563–574

Kraft CE, Kitchell JF (1986) Partitioning of food resources by sculpins in Lake Michigan. Environ Biol Fish 16:309–316

Makarewicz JC, Jones HD (1990) Occurrence of *Bythotrephes cederstroemi* in Lake Ontario offshore waters. J Great Lakes Res 16:143–147

Madenjian CP, Bunnell DB (2008) Depth distribution dynamics of the sculpin community in Lake Michigan. T Am Fish Soc 137:1346–1357

Madenjian CP, DeSorcie TJ, Stedman RM (1998) Ontogenetic and spatial patterns in diet and growth of lake trout in Lake Michigan. T Am Fish Soc 127:236–252

Madenjian CP, Hondorp DW, DeSorcie TJ, Holuszko JD (2005) Sculpin community dynamics in Lake Michigan. J Great Lakes Res 31:267–276

Mychek-Londer JG, Bunnell DB, Stott W, Diana JS, French JRP, Chriscinske MA (2013) Using diets to reveal overlap and egg predation among benthivorous fishes in Lake Michigan. T Am Fish Soc 142:492–504

Nalepa TF, Quigley MA (1980) The macro- and meiobenthos of southeastern Lake Michigan near the mouth of the Grand River, 1976-1977. NOAA data report ERL GLERL-17

Nalepa TF, Hartson DJ, Fanslow DL, Lang GA, Lozano SJ (1998) Declines in benthic macroinvertebrate populations in southern Lake Michigan, 1980-1993. Can J Fish Aquat Sci 55:2402–2413

Nalepa TF, Hartson DJ Buchanan J, Cavaletto JF, Lang GA, Lozano SJ (2000) Spatial variation in density, mean size and physiological condition of the Holarctic amphipod *Diporeia* spp. in Lake Michigan. Freshw Biol 43:107–119

Nalepa TF, Fanslow DL, Lang GA (2009) Transformation of the offshore benthic community in Lake Michigan: recent shift from the native amphipod *Diporeia* spp. to the invasive mussel *Dreissena rostriformis bugensis*. Freshw Biol 54:466–479

Nalepa TF, Fanslow DL, Pothoven SA (2010) Recent changes in density, biomass, recruitment, size structure, and nutritional state of *Dreissena* populations in southern Lake Michigan. J Great Lakes Res 36(Suppl. 3):5–19

Owens RW, Dittman DE (2003) Shifts in the diet of slimy sculpin (*Cottus cognatus*) and lake whitefish (*Coregonus clupeaformis*) in Lake Ontario following the collapse of the burrowing amphipod *Diporeia*. Aquat Ecosyst Health 6:311–323

Pettitt-Wade H, Wellband K, Heath D, Fisk A (2015) Niche plasticity in invasive fishes in the Great Lakes. Biol Invasions 17:2565–2580

Pothoven SA, Bunnell DB (2016) A shift in bloater consumption in Lake Michigan between 1993-201 and its effects on *Diporeia* and *Mysis* prey. T Am Fish Soc 145:59–68

Pothoven SA, Madenjian CP (2008) Changes in consumption by alewives and lake whitefish after dreissenid mussel invasions in lakes Michigan and Huron. N Am J Fish Manage 28:308–320

Pothoven SA, Vanderploeg HA (2017) Changes in *Mysis diluvian*a abundance and life history patterns following a shift toward oligotrophy in Lake Michigan. Fund Appl Limnol 190:199–212

Pothoven SA, Hondorp DW, Nalepa TF (2011) Declines in Deepwater sculpin *Myoxocephalus thompsonii* energy density associated with the disappearance of *Diporeia* spp. in lakes Huron and Michigan. Ecol Freshw Fish 20:14–22

Rogers MW, Bunnell DB, Madenjian CP, Warner DM (2014) Lake Michigan offshore ecosystem structure and food web changes from 1987 to 2008. Can J Fish Aquat Sci 71:1072–1086

Schaeffer JS, Bowen A, Thomas M, French JRP, Curtis GL (2005) Invasion history, proliferation, and offshore diet of the round goby *Neogobius melanostomus* in western Lake Huron, USA. J Great Lakes Res 31:414–425

Scott WB, Crossman EJ (1998) Freshwater fishes of Canada. Galt House Publications Ltd, Oakville, Ontario

Sheldon TA, Mandrak NE, Lovejoy NR (2008) Biogeography of the Deepwater sculpin (*Myoxocephalus thompsonii*), a Nearctic glacial relict. Can J Zool 86:108–115

Sell DW (1982) Size-frequency estimates of secondary production by *Mysis relicta* in lakes Michigan and Huron. Hydrobiologia 93:69–78

Truemper HA, Lauer TE, McComish TS, Edgell RA (2006) Response of yellow perch diet to a changing forage base in southern Lake Michigan, 1984-2002. J Great Lakes Res 32: 806–816

Vanderploeg HA, Nalepa TF, Jude DJ, Mills EL, Holeck KT, Liebig JR, Grigorovich IA, Ojaveer H (2002) Dispersal and emerging ecological impacts of Ponto-Caspian species in the Laurentian Great Lakes. Can J Fish Aquat Sci 59:1209–1228

Weidel BC, Walsh MG, Connerton MJ, Lantry BF, Lantry JR, Holden JP, Yuille MJ, Hoyle JA (2017) Deepwater sculpin status and recovery in Lake Ontario. J Great Lakes Res 43: 854–862

Wells L (1968) Seasonal depth distribution of fish in southeastern Lake Michigan. Fish Bull 67:1–15

Walsh MG, Dittman DE, O'Gorman RO (2007) Occurrence and food habits of the round goby in the profundal zone of southwestern Lake Ontario. J Great Lakes Res 33:83–92

Zimmerman MS, Krueger CC (2009) An ecosystem perspective on re-establishing native Deepwater fishes in the Laurentian Great Lakes. N Am J Fish Manage 29:1352–1371